Activity patterns of a synanthropic population of the brown recluse spider, Loxosceles reclusa (Araneae: Sicariidae), with observations on feeding and mating

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Abstract. I recorded diel and seasonal activity patterns and behavior of the brown recluse spider, Loxosceles reclusa Gertsch & Mulaik 1940 in a free-ranging synanthropic population in northwestern Illinois. Recluse spiders are sit-and-wait predators that spend 85–90% of their nocturnal activity sitting motionless on a small network of silk they use for prey detection. Time not spent waiting for prey is typically occupied maintaining the web by laying down new strands of silk. Feeding and sexual behavior constitute a minute, but critical, portion of daily activity. Recluses were more active at night, but some were active during the day, especially in darker areas of the garage. Activity was relatively constant during the nocturnal hours. Recluse spiders became active in early to mid-May and ceased in mid-October. Beyond this, there was no consistent pattern observed in activity through these months. Sexual encounters were typically brief and similar to behavior reported in prior lab studies. Agonism was rare, but intraspecific predation was the most significant contributor to observed mortality. The most commonly captured prey in this population were spiders (Araneae, 25%), beetles (Coleoptera, 21%) wood lice (Isopoda, 15%), and crickets (Orthoptera, 13%). Recluse spiders were never observed actively searching for prey, live or dead. More than 80% of dead prey that were offered experimentally were not scavenged. Brown recluse spiders are not active scavengers; they are sit-and-wait predators that will take advantage of dead prey they happen to encounter during other activities.

Keywords: Diel, seasonal, predation, scavenging, phenology, behavior

Despite their notoriety, the behavior of brown recluse spiders (Loxosceles reclusa Gertsch and Mulaik 1940) has not been well-studied in natural or synanthropic settings. While other species of Loxosceles have been studied in the field to a limited degree (e.g., Richman 1973; Stropa 2007; Fischer & Vasconcellos-Neto 2005), to date, behavioral studies of L. reclusa have been conducted on captive laboratory populations (Hite et al. 1966; Sandidge 2003; Sandidge & Hopwood 2005; Parks et al. 2006; Cramer 2008; Cramer & Maywright 2008) rather than on recluse spiders in natural or synanthropic populations associated with human habitation. In their seminal study of behavior and basic biology, Hite et al. (1966) stated "There was not a single paper dealing with the biology of the brown recluse" prior to their study. Hite et al. (1966) were the first to examine feeding, mating, reproduction and development, and temperature tolerance among other aspects of this medically important species, but did so entirely in a laboratory setting.

Since then, a handful of additional laboratory studies have added to our basic knowledge of brown recluse spiders. Horner & Stewart (1967) expanded on reproductive biology (growth, mortality, egg sac number, etc.) and longevity, and Elzinga (1977) followed with more on longevity showing that recluses not exposed to extreme heat could survive easily for four or more years in the lab. Eskafi et al. (1977) found that recluse spiders had extremely low rates of water loss, the third lowest of any arthropod tested to that point. Recluse spiders apparently use metabolic water because their survival was more dependent on recent feeding than ambient humidity or the percent water content of the body, which was constant at death. Cramer & Maywright (2008) proposed cold temperature as a limiting factor in naturally occurring populations of recluse spiders in Illinois, using lab temperature tolerance tests and historical winter minimum temperatures to extrapolate a hypothetical northern extent of their range that matched fairly well with their known distribution.

Sandidge (2003) renewed interest in recluse spider foraging behavior by finding that they would often eat or even prefer dead over live prey offered in a laboratory in small enclosures. However, in similar laboratory tests, Cramer (2008) found that recluse spiders preferred live prey over dead, with level of food stress, prey decay and size of live prey as other important variables influencing prey choice. Additionally, Vetter (2011a) showed that 28 of 29 non-*Loxosceles* spiders species he tested (from 11 families) would consume dead prey offered in a lab situation. Thus, Sandidge's (2003) conclusion that brown recluse spiders are unique in their ability to "actively scavenge," or that their behavior is typical in a natural setting, has been questioned.

Despite the sporadic work on brown recluse behavior over the last fifty years, there are still no published detailed behavioral studies of brown recluse spiders in the field. This study aims to begin to fill this gap and answer some basic questions about recluse spider behavior in situ. Specifically, I observed a synanthropic population of brown recluses to quantify daily activity patterns and seasonal activity, including prey choice. Additionally, I conducted in situ tests on scavenging behavior.

METHODS

Activity patterns and feeding.—Under red light, I observed brown recluse spiders in a large (20×10 m) urban garage in Monmouth, IL, USA (40.19° N, 90.64° W) from June 2013 to June 2014 when they were active (May–October). The unheated garage, 100+ years old, has double brick walls 3.3 m high with loose mortar between the two layers but no insulation and a gently sloped, wood roof peaking at 4.8 m covered by standard asphalt shingles. Although the garage has several openings for windows all but one are covered either by boards, sheet metal or both. The single glass window has a partially drawn blind and admits minimal light from the

north. The west garage door is used by the owners for their two cars and is typically left open during the day. Three vintage cars and a boat are stored in the east side of the garage and moved only once a year (in mid-summer) through a separate garage door on the east wall. In addition to the usual peripheral clutter typical of a household garage, next to the north wall there are two small (approximately 2×1 m) piles of wood and debris. Spider activity was concentrated on the peripheral floors and walls except by the garage door that was opened daily.

I focused on nocturnal observations which I divided into three observation periods of 3 h each from 21:00 to 06:00 h and supplemented with similar daytime observations. During observation periods, I alternated between focal animal sampling and scan sampling. In 10–15 minute periods, I watched groups of focal animals that ranged from 5–10 individuals (high densities and low activity allowed for more than one focal individual to be observed simultaneously). I recorded all activity to the nearest 15 sec and identified any prey items. In 45 hours of focal sampling on 15 separate dates between June and August, 2013, I totaled 278 spider-hours (one hour observing one spider) of observation. For statistical analysis and graphing, I combined focal data into eight, three-hour time periods (using start time of the focal sampling period).

Additionally, every ten minutes (between focal sampling periods), I patrolled a designated path of approximately 20 m in the area of the garage with the most spiders and scan sampled additional spiders, categorizing behavior as sedentary, web-maintenance, walking, feeding, or mating. Because spiders were not marked, some individuals were repeatedly observed. Collectively, however, I observed up to 50 individual spiders in a given 3-hour sampling period by both methods. The mean number of spiders observed by both methods was 24.4 (SE = 3.2, range 12–56), or 1.2 spiders/m², although densities in certain areas could reach 5-6 spiders/m2. I conducted additional scan sampling outside of these 3-hour sampling periods in the fall and early spring for a total of 5700 scan observations of individual spiders on 28 separate dates. After analysis, I found scan observations to be a less laborintensive yet still accurate portrayal of activity in this species. Because more observations on more individuals could be made, observations on feeding, mating, and other relatively rare activities were more likely to be made with scan sampling. I used chi-square tests to compare proportions of time spent in the various activities across sex and age. I conducted one-way ANOVAs (after arcsine transformation) to compare percent time spent in various activities across time of day and date (season).

I divided predation events into feedings observed in progress and attacks, further subdividing attacks into captures, failures, or rejections. If the prey was approached and touched, but the spider did not make an attempt at capture, I classified it as a rejection; if the spider continued to pursue but the prey evaded capture, I classified it as a failure.

Scavenging tests.—I used 3-week old crickets (Acheta domesticus) supplied by Fluker Farms (Port Allen, LA) that 1 killed by freezing. After thawing to room temperature, I placed single crickets either approximately 0.5 m or 1 m from resting recluses 90 min after sunset. I returned after 1 h and

again after 12 h to record if a spider was feeding on the prey. In 95% of cases, the cricket was either untouched or being fed on by a recluse spider. In the few instances (n = 8) when prey had disappeared after 12 h but a spider was not observed, for purposes of this test I assumed a brown recluse spider had discovered the prey and taken it out of sight to a retreat. I observed several instances where reeluse spiders had moved the prey up to 30 cm. Although some disappearances may have been due to ants, which I observed disassembling and removing prey in one instance, I saw no evidence of miee or other scavengers or predators in the garage interfering with these tests. I used chi-square tests of independence to examine the effects of distance (of prey from a spider) and time of exposure on scavenging frequencies.

RESULTS

Activity patterns.—Overall, scan observations reveal that recluse spiders spent 88% of observed time sitting in wait for prey. Considering that recluses do not move during feeding, recluses spent 92% of their time motionless. Web maintenance (8%) consisted of slow, methodical movements laying down new strands of silk in a roughly circular area typically less than 30 cm in diameter. Other activities such as walking distances greater than 0.5 m, mating, and agonistic encounters were rarely observed. Focal observations reveal nearly identical statistics with 87% of observed minutes sitting in wait for prey, and 92% either waiting or feeding.

Influence of sex and age on activity: Male and female brown recluses showed the same level of overall activity ($\chi^2 = 2.1$, df = 1, P = 0.15), with females slightly more active (17.3%) than males (13.7%). However, much of the slight difference in female activity was due to their higher incidence of feeding. Removing feeding effectively eliminated any minor difference between male (11.3%) and female activity (10.6%). In contrast, juveniles were much less active than adults, spending scarcely 5% of their time active ($\chi^2 = 54.0$, df = 1, P < 0.0001).

Diel patterns: Scan observations showed that recluses were largely, but not exclusively, nocturnal. Fewer reeluses were observed during the day, and they were even more sedentary (Fig. 1A). Nocturnal activity levels averaged nearly 14% while daytime activity averaged approximately half that ($\chi^2 = 35.6$, df = 7, P < 0.0001). Although recluses may feed for hours on a single prey item, removing feeding as an activity did not change these diel patterns ($\chi^2 = 32.4$, df = 7, P < 0.0001). Most of the individuals observed to be active during the day were found in the darker recesses of the garage, far from the door which was typically left open during daylight hours.

Focal observations confirmed the basic pattern of higher activity at night (Fig. 1B), particularly from 0:00–6:00 h. Recluses were nocturnally active for about 13% of observed minutes compared to less than 8% activity during daylight hours (ANOVA, F=6.8, df = 7, P<0.0001) and this trend was more pronounced when removing feeding activity (F=8.0, df = 7, P<0.0001). Much of the observed daylight activity was feeding, probably on prey captured at night with protracted feeding times extending into daylight hours.

Seasonal patterns: Spiders were not active at all between mid-October and mid-April, but presumably were hibernating in abundant refugia within the garage (e.g., in large, deep cracks in the foundation, under or in stored items). From scan

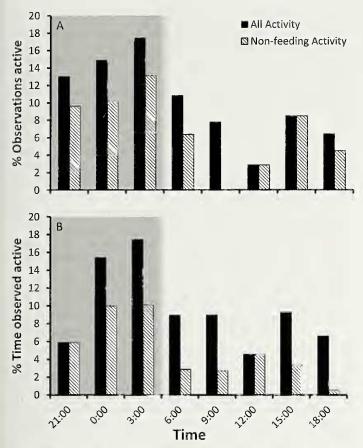


Figure 1.—Diel activity patterns in brown recluses. A. Scan observations. B. Focal observations. Shaded area corresponds to approximate nocturnal hours.

observations over the 5 months of peak activity divided into 2-week periods, brown recluses showed significant seasonal variation in activity ($\chi^2 = 32.3$, df = 9, P = 0.0002). While their activity seemed somewhat periodic (Fig. 2), activity varied from an average of 11-17% and was not correlated with daily high (r = -0.16, P = 0.42) or low (r = -0.07, P = 0.73) temperatures (Illinois State Climatological Office records for Monmouth, IL). Similarly, lunar cycles did not correspond to peaks or troughs in activity.

Mating and agonistic interactions.—I observed 19 mating attempts (four during focal sampling and 15 in scan samples) and of these three failed. In the four focal mating attempts (where the entire interaction was observed) the total interaction time varied from 2:20 to 9:00 min. Precopulatory behavior consisted of tapping with the forelegs, stroking of the female with forelegs, and drumming or stridulating with palps as previously described (Hite et al. 1966; Horner & Stewart 1967). One to four intromissions were typical in a single mating attempt, although in one pair 13 intromissions occurred. Notably, the male in this interaction was in very poor condition with a visibly shriveled abdomen. The duration of intromissions varied from 1 to 13 sec with a standard deviation (3.1 sec) greater than the mean (3.0 sec). Briefer intromissions of 1 sec or less appeared to be tentative approaches before actual sperm transfer during the final, and usually longest, intromission. In only one case was the final intromission shorter than prior attempts. The final

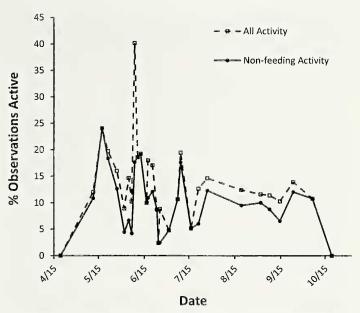


Figure 2.—Seasonal activity patterns in brown recluses from scan observations.

intromission averaged 5.8 sec, significantly longer than preliminary attempts averaging 1.7 sec (t = 3.98, df = 15, P = 0.001). After the final intromission, the male quickly separated and ran rapidly to 0.5 m or more away from the female.

Only five agonistic encounters were observed, four of these during focal animal sampling. Encounters were typically very brief, lasting less than five seconds and involving tapping with the forelegs, often followed by a rapid retreat of one individual, in two cases, the much smaller spider.

Feeding.—I observed 81 prey encounters (spiders feeding or attacks in progress), 63 during scan sampling and 18 during foeal sampling. While I observed fewer predation events in focal sampling, more actual attacks were recorded by this method. Of all prey encounters observed by both methods, most observations were of spiders already feeding (n = 64) while the remainder (n = 17) were in the midst of attacks or approaches.

The most common prey items successfully captured or being fed upon were other spiders (25%, n=17) with other brown recluses (n=7) the most prevalent. Beetles (principally Carabidae) were nearly as frequently preyed upon (21%). Wood lice (Isopoda) were also commonly encountered but were less successfully preyed upon (15%), while crickets (Orthoptera) and moths (Lepidoptera) were also often victimized (13 and 9% respectively). Of the 17 attacks observed in progress, only three prey were successfully captured while three were rejected. In the 278 hours of focal observations, I never observed a spider scavenging on naturally available dead prey.

Scavenging trials.—Of all prey offered (n=146), spiders found only one in six (17%). One in four prey (24%) placed within 0.5 m of a visible spider were found within 12 hours, but less than half that (11%) were discovered if placed 1 m from a visible spider ($\chi^2 = 4.2$, df = 1, P = 0.04). Many more prey were found after 12 h (14%) than after 1 h (3%) at both

distances ($\chi^2 = 16.9$, df = 1, P = 0.0002). On several occasions, a cricket placed within 0.5 m of multiple spiders (up to four) was left untouched. I observed no differences in scavenging frequency between males (n = 6) and females (n = 8) or juveniles (n = 11) and adults (n = 14).

DISCUSSION

The brown recluse spider's overall low levels of activity are consistent with its sit-and-wait predation lifestyle and prior studies on its longevity (Hite et al. 1966; Elzinga 1977), hardiness (Eskafi et al. 1977) and extremely low metabolic rate (Carrel & Heathcote 1976). In light of this study, the common knowledge that the brown recluse spider is largely nocturnal is perhaps better described as negatively phototaxic, as spiders in this study were often observed to be active during the day in low light conditions. Given the low cost of their inactive lifestyle, being out of a retreat during the day but still in darkness (e.g., caves, garages, attics, basements) would probably cause little increase in predation risk, particularly because nearly all the mortality that I observed was due to intraspecific predation.

The similarity in male and female activity levels contradicts conventional wisdom that males wander more and widely as they are often caught in sticky traps. However, my observations are biased against capturing many long-distance movements, which could be infrequent, but significant. Also, the few long movements I did observe were, in fact, mostly males. Studies of individually marked spiders currently underway should shed more light on infrequent, but longer distance movements by recluses. Juvenile activity may be far lower simply as a result of their smaller size and thus smaller webs to construct and maintain. Alternatively, juveniles may also be more at risk of death due to starvation so that movements are avoided as a means of conserving energy.

The seasonal activity of recluse spiders recorded here (May-October) is consistent with that gleaned from records of submissions of samples from the public which peak between May and August (Vetter 2011b). Vetter (2011b) suggested that the apparently regular seasonal activity of recluses even in temperature-controlled human habitat indicated a photoperiod dependency. Lending some support to this hypothesis, in this study brown recluses were not abundant until at least four weeks after nighttime temperatures had increased to 10°C, well above that of the 5°C minimum required for activity according to Hite et al. (1966).

The mating behavior I observed was similar to that recorded by Hite et al. (1966) in the lab. They recorded multiple intromissions (up to 11 times) as well, with some lasting 20 to 30 sec. Horner & Stewart (1967) also found that pairs would engage in up to nine intromissions, but did not report durations. Curiously, in one of the four mating attempts that Hite et al. (1966) detailed, the duration of intromission decreased with each subsequent attempt, the opposite of what I observed in six of nine interactions with multiple intromissions.

Considering the high density of spiders in some areas, the low number of agonistic encounters reflects the sedentary nature of brown recluses, and possibly mechanisms whereby they can avoid other individuals when they are moving. However, the relatively high rate of intraspecific predation

(seven instances in 67 suecessful predation events) suggests that while agonism is rare, it can have significant consequences. Stropa (2007), in staged lab encounters of *L. gaucho* males, found that only 22% of interactions were aggressive (lunges or bites); the vast majority of interactions (77%) were non-aggressive. He attributed this to the dense populations of the spider and possible sociality. Vetter & Rust (2008) also noted that agonism among juveniles reared in the lab is rare if they are supplied with ample food. Alternatively, in a non-lab situation where food is scarce, generally low levels of aggression could be a mechanism whereby smaller spiders reduce their risk of mortality from intraspecific predation.

Like most spiders, brown recluse spiders appear to be opportunistic predators. In this study, recluse spiders fed on conspecifics and other spiders, isopods, beetles, crickets, and moths. These arthropod groups were also the potential prey that I most commonly observed in the garage. Hite et al. (1966) reported a wide variety of arthropods found in webs of brown recluses without commenting on relative frequency of prey or their abundance. Richman (1973) studying a related species (L. arizonica) found principally ants captured in webs, which were also very common at his study site in the Sonoran desert. Fischer et al. (2006) also reported that isopods and beetles were common prey in webs of the South American species L. intermedia in both homes and forested habitat. In contrast to my study, arachnids were rarely reported (though commonly collected nearby) as prey, and various hymenoptera, especially ants, were common prey.

Since Sandidge's (2003) assertion that brown recluses "actively search for dead prey" and actually prefer dead to live prey, two publications have cast doubt on his hypothesis. Cramer (2008) replicated Sandidge's (2003) lab tests taking into account three influential variables: live prey size, dead prey quality, and the spider's level of hunger. I found that brown recluse spiders preferred live over dead prey, fresher over more decomposed prey when scavenging, and that starved spiders would take more risks attacking large, live prey than would well-fed spiders. My observations of predation in the garage showed that recluse spiders were not hesitant to attack live prey (though often unsuccessfully), contrary to Sandidge's (2003) findings that recluses often fled from live prey. Combining these findings with Vetter's (2011a) observations that 99% of non-Loxosceles spider species he offered dead prey in a lab situation would consume it, and observing that brown recluse spiders seldom move more than half a meter in a night led to my in situ tests on scavenging. My tests confirm that while brown recluse spiders will scavenge given the opportunity, the likelihood of them encountering dead prey is low unless the prey dies very close to a resident spider. As suggested by Sandidge (2003), it is conceivable that a large influx of dead prey from pest control efforts could provide a pulse of potential prey to a dense population of brown recluse spiders. However, given that 1) spiders found only 20% of dead prey in this study, 2) the desirability of dead prey declines rapidly with age (Cramer 2008), and 3) a single prey item is often sufficient to take a recluse spider through its next molt such that many dead prey killed by pesticide application would be of low quality after a few days, the potential impact of such a scenario on overall population size

is far from certain without controlled, manipulative field experiments on multiple populations.

While this study focused on a single synanthropic population in an urban garage, my observations support anecdotal reports on the behavior of this species and it seems that some general conclusions can be made with respect to spiders living in association with humans. Brown recluse spiders are sit-andwait predators that expend very little energy on prey capture beyond the costs of web construction and maintenance. Once they emerge from winter retreats, levels of activity do not vary predictably across seasons. Likewise, there is no pattern in their nocturnal activity, and they can be and are active diurnally under low light conditions. Mating behavior in the wild is similar to that recorded in the lab, and agonistic encounters are rare. Brown recluse spiders appear to be nonselective predators that will consume whatever live arthropod prey stumble into their webs that they are capable of subduing. They do not actively search for either live or dead prey, but will feed on dead prey if they discover it in their immediate vicinity. Future behavioral observations of recluse spiders in natural habitats would be a welcome contribution to knowledge of this medically important species.

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